FRESHWATER ECOLOGY

The effects of nutrient enrichment and invasive mollusks on freshwater environments

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Abstract. The effects of an invasive species on the environment can be altered by anthropogenic activities such as nutrient pollution or the presence of additional invasive species with similar or unique traits. Using experimental mesocosms, we tested the separate and combined effects of three invasive mollusks (zebra mussels, Asian clams, and banded mystery snails) on freshwater environments in nutrient-poor and nutrient-enriched conditions. We predicted that in nutrient-poor conditions, single mollusk species would reduce the abundance of algae and zooplankton, but nutrient enrichment would mitigate these effects. Regardless of nutrient additions, paired bivalve species would reduce phytoplankton and zooplankton abundance, increasing periphyton biomass. Bivalves and snails paired together would reduce periphyton, phytoplankton, and zooplankton compared to communities with paired bivalve species. Finally, nutrient enrichment would increase the survival or biomass of paired bivalves and snails. Single, paired, and three co-occurring invasive mollusks did not affect algae or zooplankton abundance. Banded mystery snails reduced nutrient concentrations in high-nutrient conditions more than other invasive species, but the reduced nutrients did not affect algal abundance. Paired invasive species did not affect the survival or biomass of other invasive species. Nutrient enrichment increased the biomass of zebra mussels and mystery snails, but not Asian clams. Additionally, zebra mussel reproduction increased in the high-nutrient treatment when banded mystery snails were present, but not when all three species were together. We conclude that human-induced trophic states might determine the effects that single and multiple invasive species have in freshwater environments.

Key words: non-indigenous species; non-native species; nutrient pollution; phytoplankton; total nitrogen; total phosphorus.

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INTRODUCTION

Humans have intentionally or unintentionally influenced the movement and distribution of species across the world, leading to biological invasions, environmental change, and economic loss (Ricciardi 2007, Ricciardi et al. 2013). Mixed results regarding the ecological and evolutionary impacts of invasive species have delayed the development of a mechanistic understanding of how and when invasive species affect freshwater systems (Ricciardi 2005, Armitage et al. 2009,

DeVanna et al. 2011, Jeschke et al. 2012, Jeschke 2014, Jackson 2015, Henriksson et al. 2016). Anthropogenic activities such as nutrient pollution might determine the magnitude and impacts of single and multiple invasive species on freshwater environments, explaining the mixed effects observed in ecological and evolutionary studies (Gurevitch and Padilla 2004, Didham et al. 2005, Jeschke et al. 2012, Jeschke 2014, Jackson 2015).

Many freshwater systems contain more than one invasive species, leading to complex interactions that alter environmental conditions (Preston et al. 2012). A lack of understanding of these complex interactions could lead to difficulty in developing predictive models of invasive-species impacts (Jackson 2015). A single invasive species can have negative, neutral, and positive ecological effects across habitats or ecosystems (e.g., the snail *Potamopyrgus antipodarum*; Schreiber et al. 2002, Kerans et al. 2005, Riley et al. 2008). Multiple invasive species might have weak effects on their environment due to competition for limited resources, or strong effects due to facilitative interactions or an increased density of consumers (Gallardo and Aldridge 2015, Jackson 2015).

The effects of single or multiple invasive species might depend on anthropogenic effects (Rahel and Olden 2008), such as nutrient pollution in freshwater ecosystems (Camargo and Alonso 2006). Increased productivity due to nutrient pollution (Smith 2006) can also alter the individual and combined effects of invasive species. For example, invasive carp (*Cyprinus carpio*) have stronger negative ecosystem effects in shallow, high-nutrient lakes compared to low-nutrient lakes (Weber and Brown 2011). Nutrient pollution should also increase the success of filter-feeding invasive species due to an increased density of food resources (e.g., phytoplankton). Nutrient additions could allow for sustained high-density populations of invasive filter feeders, despite the typical shift in the energy pathway from pelagic to benthic, that might limit the population size of invasive bivalves (Higgins and Zanden 2010, Gallardo et al. 2016, Kovalenko et al. 2017). Additionally, invasive filter feeders have very high filtration rates (Fanslow et al. 1995), allowing for the exploitation of phytoplankton resources, which can have cascading ecological effects in freshwater environments (Stewart and Haynes 1994, Strayer et al. 1999).

Nutrient pollution could allow for continuous algal blooms, sustaining invasive bivalves that have high filtration rates. Therefore, the combined effects of nutrient pollution and invasive mollusks could cause declines in zooplankton abundance or biomass and potentially reduce species richness and diversity. Despite field studies showing declines in zooplankton, results from experimental studies indicate that the effect of invasive species is not dependent on nutrient pollution (Sinclair and Arnott 2015). Given the mixed results, the potential interactive effects of multiple invasive mollusks and nutrient pollution on freshwater environments remain unclear, highlighting the need for an experimental approach assessing how invasive mollusks interact, and if those interactions are altered by nutrient pollution.

Three common invasive mollusk species in freshwater systems in North America are the zebra mussel (*Dreissena polymorpha*), Asian clam (*Corbicula fluminea*), and the banded mystery snail (*Viviparus georgianus*). All three species can co-occur in freshwater lakes and rivers in Eastern North America (e.g., the Hudson River, Mississippi River, Lake Erie, and Lake George, New York, USA). Zebra mussels and Asian clams are considered two of the most pervasive and damaging invaders of freshwater ecosystems in Europe and North America (Warwick Fisher et al. 1991, Hornbach 1992, Gurevitch and Padilla 2004, Sousa et al. 2008). Banded mystery snails are native to southeastern North America but have spread widely throughout the United States in the last century (Bury et al. 2007). Despite being a widespread invasive species, the effects of this snail on freshwater organisms and ecosystems across its invaded range are largely unknown (but see Jokinen et al. 1982). Zebra mussels and Asian clams primarily filter phytoplankton from the water column, but Asian clams can feed on periphyton and soil microbes through pedal feeding (Hakenkamp et al. 2001, Pigneur et al. 2014, Vaughn and Hoellein 2018). Invasive bivalves such as zebra mussels and Asian clams often have very high filtration rates, and selective feeding that can alter the nutrient distribution in the environment, and the abundance and composition of phytoplankton species (Higgins and Zanden 2010, Vaughn and Hoellein 2018). The reduction in phytoplankton can

reduce food resources for zooplankton populations and alter the nutrient pathway from pelagic to benthic, increasing the opportunity for benthic plants (Vaughn and Hoellein 2018).

Banded mystery snails often graze periphyton from the benthos. This consumption could increase the quantity of recycled nutrients in the water column (Hansson 1990), which could increase the quantity of phytoplankton for filter feeders (e.g., invasive clams and mussels). Therefore, snails and nutrient pollution might equally benefit invasive mollusks. Alternatively, large Viviparidae snails egest 30–50% of their food intake (Hunter 1975). Egestion of food would lock nutrients away from zebra mussels, but could increase food resources for Asian clams, since they filter feed and pedal feed. Understanding the individual and combined effects of these invasive species under varying nutrient conditions can offer insights into how these common invasive species affect biotic and abiotic aspects of freshwater environments (Hintz et al. 2019).

To understand the individual and combined effects of three invasive mollusks, and to test whether their effects on freshwater environments are dependent on trophic state, we experimentally manipulated the presence and co-occurrence of zebra mussels, Asian clams, and banded mystery snails under two nutrient levels (oligotrophic or eutrophic). We assessed the effects invasive mollusks have on abiotic conditions (e.g., dissolved oxygen [DO] and nutrient concentrations) and on biotic responses (e.g., algal abundance, zooplankton richness, and zooplankton density. We predicted that (1) invasive filter feeders (i.e., Asian clams and zebra mussels) would reduce phytoplankton abundance, zooplankton density, and zooplankton richness under oligotrophic conditions; (2) eutrophic conditions would ameliorate negative effects that the individual invasive bivalves had on the planktonic community; (3) regardless of trophic state, co-occurring Asian clams and zebra mussels would reduce phytoplankton and zooplankton, and increase periphyton biomass that would be available for grazing species; (4) co-occurring bivalves and snails would reduce periphyton, phytoplankton, and zooplankton compared to communities with paired bivalve species (i.e., an invasional meltdown; Simberloff and Von Holle 1999); and (5) co-occurring bivalves and snails in

nutrient-enriched treatments would have high individual biomass and survival due to positive nutrient feedback loops.

Materials and Methods

We conducted the experiment at the Rensselaer Aquatic Lab (Troy, New York, USA). We tested invasive species alone, paired, and all three together, in either low or high nutrients (i.e., 16 total treatments). For these experiments, we used cylindrical 750-L polyethylene cattle tanks (i.e., mesocosms) covered with 60% shade cloth to prevent oviposition by terrestrial invertebrates and amphibians; each treatment was replicated five times for a total of 80 experimental units. The mesocosms are exposed to natural variations in environmental conditions, closely mimicking the temperature of a nearshore community in a small lake (approximately 25.0–28.0°C).

To simulate oligotrophic conditions, we filled the mesocosms on 15 June 2015 with water collected from Lake George, New York, USA. From the offshore chemistry survey conducted at Lake George on 16 June 2015, the total nitrogen (TN) concentration near the site of water collection was 0.11 mg/L, and the total phosphorus (TP) concentration was measured to be 3.7 µg/L (Hintz et al. 2020). On 17 June, we added 7.5 cm of bank-run river sand to serve as a substrate and on 26 June placed three 7.6 × 15.2 cm ceramic tiles vertically in the mesocosms as a standardized surface for measuring periphytic biomass. On 27 June, we added 300 mL of concentrated zooplankton and phytoplankton collected from Lake George, New York. We obtained a dense zooplankton stock by allowing an 80-µm zooplankton net to drift for 100 m 5–10 m below the surface of the water. We added a second 300-mL aliquot of zooplankton and phytoplankton on 8 July (collected the same way as on 27 June), to ensure that each mesocosm received a sufficient number of each zooplankton species to establish viable populations. Each zooplankton aliquot was visually inspected, and any unwanted zooplankton predators were removed (e.g., insect larvae and fish).

Ten days after the initial addition of zooplankton and phytoplankton, we added the invasive species to all mesocosms, except for those

assigned to the control treatments (i.e., zero invasive species), defining this as day 0 of the experiment. We added 25 individuals of each invasive species to any mesocosm designated to contain that species. As a result, mesocosms assigned zero, one, two, and three invasive species received a total of 0, 25, 50, or 75 individuals. The mass of the organisms is not indicative of filtering rate, because zebra mussels have a thinner shell than Asian clams, so we normalized by the number of individuals. We only used 25 individuals of each invasive species to avoid having too high of densities of invasive species, which might have led to unrealistic results that would not be expected in natural communities. This could have occurred at high densities because invasive filter feeders have very high filtration rates (Fanslow et al. 1995), which could have allowed for the exploitation of phytoplankton resources (Stewart and Haynes 1994, Strayer et al. 1999). The loss of phytoplankton groups from the mesocosms would have led to drastic reductions in zooplankton communities, which would be unrealistic because most natural systems would have some sort of dispersal mechanism to replenish phytoplankton and zooplankton species that are lost locally to invasive mollusks.

The additive design used in this experiment is appropriate to test how anthropogenic modification of the trophic state alters the impacts of individual and multiple with similar or different traits (Johnson et al. 2009); however, this experimental design is not appropriate for testing how varying densities of invasive species affect freshwater ecosystems. The additive experimental design allowed us to test individual invasive species and combined invasive species, but did not allow us to understand whether more invasive individuals of the same species would lead to a similarly observed result as the treatment with 25 individuals of three invasive species (75 total). Therefore, our interpretation of the data is limited to the effects of the nutrients on the individual and combined invasive species.

We allowed the organisms to acclimate in their assigned mesocosms for 24 h before we applied the nutrient treatment to half of the mesocosms. After 24 h, we increased the concentration of total phosphorus (TP) to 100 μg/L, using lab-grade potassium phosphate (KH_2PO_4) and the concentration of total nitrogen to 1600 μg/L,

using lab-grade potassium nitrate (KNO_3), to maintain a molar N:P ratio near 35:1. These nutrient additions were based on previous experimental nutrient additions (Shurin 2001, Schuler et al. 2015) and changed the trophic state of the high-nutrient mesocosms from oligotrophic to eutrophic. We added nutrients a second time on 24 July. To avoid increasing potassium in the mesocosms, we used lab-grade sodium phosphate ($NaPO_4$) and lab-grade sodium nitrate ($NaNO_3$) but added the same amount of phosphorus and nitrogen (100 and 1600 μg, respectively) maintaining a N:P ratio of 16:1.

We collected banded mystery snails from Glass Lake near Troy, New York, and zebra mussels from a pooled reach of the Mohawk River, near Troy. We collected Asian clams from Lake George. Prior to introducing each invasive species into mesocosms, we size-sorted and kept them in wading pools for at least 48 h to avoid adding any individuals that might have died due to our collection methods. For the 25 individuals of each species added to an assigned mesocosm, we introduced 20 small (10–15 mm) and 5 large (15–25 mm) banded mystery snails, 20 small (10–15 mm) and 5 large (15–25 mm) Asian clams, and 25 large (12–20 mm) zebra mussels. We added differently sized individuals to observe changes in biomass, changes in survival, and changes in reproduction among the treatments. Adding only small or large individuals might limit the potential changes that could be observed during the experiment.

Data collection

Given that changes in abiotic factors can be indicators of reduced water quality, we measured pH, temperature, and dissolved oxygen (DO) on days 9, 13, 20, and 84 (16 July, 20 July, 27 July, and 29 September). More samples were taken in the beginning of the experiment to capture changing water conditions after the introduction of invasive species and nutrients. On 2 October (day 87), we assessed the remaining nutrient levels—total nitrogen (TN) and total phosphorus (TP)—in each mesocosm to determine how nutrient levels in the water column might be altered by each invasive-species treatment. We obtained water from the center of each mesocosm using two 50-mL centrifuge tubes; one sample was used for TN analysis and the other was used for

TP analysis. Samples were flash-frozen in a −80 freezer and transported to the Darrin Fresh Water Institute (DFWI; Bolton Landing, New York, USA) for analysis using persulfate digestion (Langner and Hendrix 1982, Hintz et al. 2020).

We also measured biotic factors during the experiment, including periphyton, phytoplankton, and zooplankton. We measured periphyton on days 21 and 87 (28 July and 2 October). For each sample, we brushed all periphyton from a single ceramic tile from each mesocosm using distilled water (Rodgers et al. 1996). We filtered the algae from the water using a pre-dried and pre-weighed glass fiber filter (GF/C filters; Whatman, Maidstone, UK). We then dried filters for 24 h at 60°C and weighed (to the nearest mg) them to determine periphyton biomass.

We collected phytoplankton samples on days 10, 21, and 84 (17 July, 27 July, and 29 September). We measured phytoplankton abundance as the concentration of chlorophyll *a* (chlA) in the water column. To estimate chlA, we collected 500 mL of water from the center of each mesocosm 15–20 cm below the surface of the water. We filtered the phytoplankton from the water using GF/C filters, covered the filters in aluminum foil, and frozen them for analysis using fluorometry after extraction with 90% acetone (Arar and Collins 1997).

We sampled zooplankton on days 21 and 87 (27 July and 2 October). To sample zooplankton, we collected 1000 mL of water from five standardized locations in each mesocosm (5 L total). After homogenizing the samples from each mesocosm, we concentrated zooplankton by filtering the samples through an 80-μm net. We preserved zooplankton by adding 5–10 drops of Lugol's iodine to each centrifuge tube (Dodson et al. 2000, Schuler et al. 2017*b*) and later estimated the abundance of each species, which we used to calculate the density of individuals, species richness, and species diversity.

Fall months produce cold-water conditions that slow or stop invertebrate growth; therefore, we terminated the experiment on 2 October, which was 87 d after adding the invasive species to the mesocosms. To test whether the invasive species reproduced, we haphazardly searched for juvenile clams and snails by running a 0.5-mm sieve through the center of 10 mesocosms

containing those invasive species. We then recovered the stocked individuals of the three invasive species by filtering all of the water and sand from each mesocosm through a 10-mm sieve. Each individual was larger than 10 mm at the beginning of the experiment, so all remaining live individuals were captured. We preserved the invasive species in 70% ethanol for later enumeration and measurements. We determined survival by examining the shell and muscle tissue of each individual. If a shell was void of muscle tissue, we classified the individual as having died during the experiment and did not include it as a survivor. We then calculated the percent survival for each species in each mesocosm by dividing the total number of surviving individuals by the total number of individuals that we added to the mesocosms. We estimated the average individual mass for each invasive species as the oven-dried total mass (24 h at 60°C) divided by the number of surviving individuals captured from each mesocosm. Due to a sorting error, we could not estimate the survival and individual biomass of zebra mussels from one low-nutrient, three-species mixture replicate and one high-nutrient, zebra mussel monoculture replicate.

Although we did not observe reproduction by banded mystery snails or Asian clams, we did observe reproduction by zebra mussels. We estimated their reproduction by counting the number of settled veligers (juveniles) that were attached to one 7.6 × 15.2 cm ceramic tile in each mesocosm.

Statistical analyses

We conducted all analyses using R version 3.4.0 (R Core Team 2017). For each zooplankton sample collected from the mesocosms, we calculated zooplankton species richness and density. We used the estimates of density and richness to calculate species diversity (ENS$_{PIE}$) for each sample using the *diversity* function in the vegan package in R (Oksanen et al. 2016). ENS$_{PIE}$ is calculated from Hurlbert's probability of interspecific encounter (PIE), which is a method of rarefaction that is largely independent of the number of individuals sampled (Schuler et al. 2015, 2017*a*), and is similar to Simpson's index (where Simpson's index is D, and PIE is $1 − D$). To fully represent diversity, PIE must be converted to a true diversity metric (i.e., effective

number of species or ENS_{PIE}; Jost 2006). ENS_{PIE} allows for the comparison of relative abundance distributions due to a treatment effect within a single species pool (Dauby and Hardy 2012, Chase and Knight 2013, Schuler et al. 2017*a*).

To test the effects of nutrients and invasive species on response variables measured more than once, we used linear mixed-effects models (LMM; Hickey et al. 2018). We tested the assumptions of normality and homogeneity of variance for each response variable using QQ plots with complimenting Shapiro test and Bartlett tests. Data that did not meet the assumptions of normality and homogeneity of variance were log-transformed and re-tested for normality. We used the lme4 package to conduct the LMMs, with the treatments and time as fixed factors, and mesocosm number as a blocking factor. We used eight LMM models that tested for the effects of each independent treatment and interactions among treatments (Appendix S1: Table S2). We then used the *anova* function to obtain AIC scores for each model (Appendix S1: Table S3). We selected the LMM model with the lowest AIC score for each response variable and used the lmerTest package and the car package to obtain approximate F and P values for that model.

We used generalized linear models (*glm* function) to analyze factors measured once during the experiment (TN, TP, mass, survival). We tested the assumptions of normality and homogeneity of variance for the mass and nutrient response variables using QQ plots with complimenting Shapiro test and Bartlett tests. Data that did not meet the assumptions of normality and homogeneity of variance were log-transformed and re-tested. Nutrient data were analyzed using the *glm* function, with only the invasive-species treatments as the predictor variables, to avoid having nutrients as a response and predictor variable in the same model. To understand whether the survival of each species was affected by the presence of another invasive species or nutrients, we used the *glm* function with a quasi-binomial distribution (i.e., logistic regression). For the TN and TP analyses, we used Dunnett's tests to compare each invasive-species treatment back to the corresponding control treatment (low or high; Appendix S1: Table S1).

RESULTS

Abiotic measurements

Temperature, dissolved oxygen (DO), and pH were not affected by the invasive-species treatments (Table 1). Temperature changed over time, but did not differ among any other treatments (Table 1). Dissolved oxygen and pH were affected by nutrient additions and time, but these changes were likely due to fluctuations in phytoplankton biomass (Table 1). The average DO among the treatments was higher in high-nutrient mesocosms and was higher in September than in the three samples taken in July (Appendix S1: Fig. S1).

The final concentration of TN and TP was affected by the presence of the invasive species, but only in the high-nutrient treatments (Table 1, Fig. 1; Appendix S1: Table S1). Compared to the high-nutrient control, TN was lower in mesocosms containing clams ($P = 0.037$), snails ($P = 0.001$), snails and clams ($P = 0.012$), snails and mussels ($P = 0.001$), and all invasive species combined ($P = 0.004$; Appendix S1: Table S1; Fig. 1). Similarly, compared to the high-nutrient control, TP was lower in mesocosms containing snails ($P = 0.032$), snails with clams ($P = 0.001$), snails with mussels ($P = 0.001$), and all invasive species combined ($P = 0.005$; Appendix S1: Table S1; Fig. 1).

Biotic measurements

Periphyton biomass was affected by time and nutrients, but there was no effect of invasive species or any interactions among treatments (Table 2; Appendix S1: Fig. S2). Periphyton biomass (averaged across all sample dates, ± 1 standard error [SE]) was 0.14 ± 0.02 mg per tile in the high-nutrient treatment vs. 0.09 ± 0.01 mg per tile in the low-nutrient treatment.

Phytoplankton (i.e., chlA concentration) was affected by nutrients and time, and there was a nutrient-by-time interaction, but no effect of invasive species or any other interaction among treatments (Table 2, Fig. 2). The nutrient-by-time interaction occurred because there was a large increase in phytoplankton in the high-nutrient treatment relative to the low-nutrient treatment on the first sample date, a modest increase on the second sample date, and no difference in phytoplankton between the high- and low-nutrient

Table 1. Results from each repeated-measures ANOVA for abiotic response and the results from the ANOVA for total nitrogen (TN) and total phosphorus (TP), which were only measured once at the end of the experiment.

Treatment	Temperature		pH		DO		TP		TN	
	F	P	F	P	F	P	F	P	F	P
Nutrients (N)	–	–	$16.472_{1,78}$	**0.001**	$39.432_{1,78}$	**0.001**	–	–	–	–
Species (S)	–	–	–	–	–	–	$4.327_{7,64}$	**0.001**	$2.785_{7,64}$	**0.014**
N × S	–	–	–	–	–	–	–	–	–	–
Time (T)	$8835.7_{3,237}$	**0.001**	$22.501_{3,234}$	**0.001**	$238.362_{3,234}$	**0.001**	–	–	–	–
N × T	–	–	$1.389_{3,234}$	0.247	$7.353_{3,234}$	**0.001**	–	–	–	–
S × T	–	–	–	–	–	–	–	–	–	–
N × S × T	–	–	–	–	–	–	–	–	–	–

Notes: DO, dissolved oxygen. Invasive species did not alter the abiotic conditions of the mesocosms, with the exception of the ending nutrient (TN and TP) concentrations in the mesocosms. Values in subscript are df values. P values in boldface indicate statistical significance ($P < 0.05$). Models with corresponding F and P values had the lowest AIC scores, whereas models with dashes had higher AIC scores and were not included in the analysis.
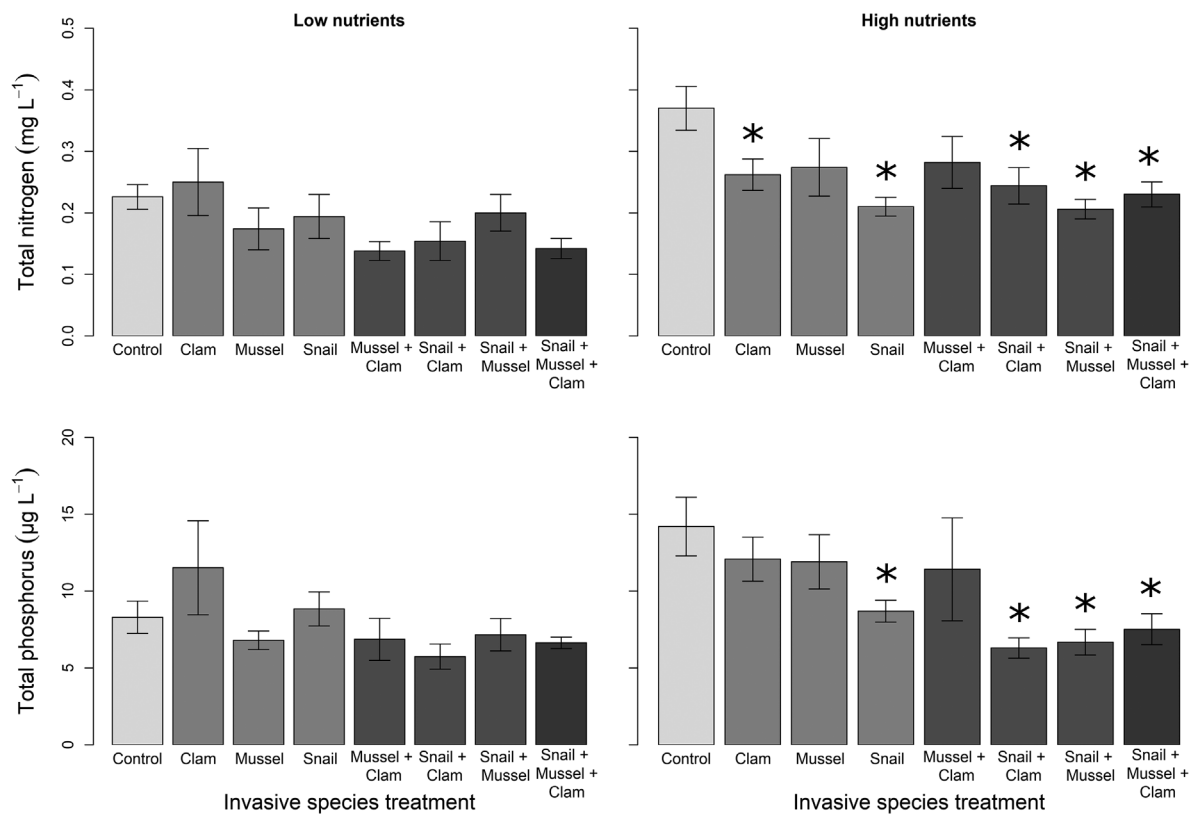

Fig. 1. The final concentration of total nitrogen (top) and total phosphorus (bottom), in each invasive-species treatment, in low-nutrient (left) or high-nutrient (right) conditions. The asterisks indicate significant differences from the control in each treatment. Error bars indicate ± 1 standard error around the mean.

treatments between treatments on the third sample date.

Zooplankton density (Appendix S1: Fig. S3) increased in the nutrient addition treatments, but was not affected by invasive species, time, or any treatment interactions. Zooplankton richness was higher in the nutrient addition treatments (Appendix S1: Fig. S4), and species richness was

Table 2. Results from each repeated-measures ANOVA for biotic response.

Treatment	Phytoplankton		Periphyton		Zooplankton density		Zooplankton richness		Zooplankton diversity	
	F	P	F	P	F	P	F	P	F	P
Nutrients (N)	$29.495_{1,78}$	**0.001**	$4.345_{1,78}$	**0.032**	$19.010_{1,76}$	**0.001**	$7.740_{1,76}$	**0.006**	–	–
Species (S)	–	–	–	–	–	–	–	–	–	–
N × S	–	–	–	–	–	–	–	–	–	–
Time (T)	$204.757_{2,156}$	**0.001**	$31.406_{1,78}$	**0.001**	$7.410_{1,76}$	**0.008**	$45.994_{7,76}$	**0.001**	$7.070_{1,76}$	**0.010**
N × T	$9.217_{2,156}$	**0.001**	–	–	–	–	–	–	–	–
S × T	–	–	–	–	–	–	–	–	–	–
N × S × T	–	–	–	–	–	–	–	–	–	–

Notes: Nutrients additions altered the biotic aspects of the communities in the mesocosms more than the invasive species. No significant effects of invasive species on the biotic community were observed in this experiment. Values in subscript are df values. P values in boldface indicate statistical significance ($P < 0.05$). Models with corresponding F and P values had the lowest AIC scores, whereas models with dashes had higher AIC scores and were not included in the analysis.
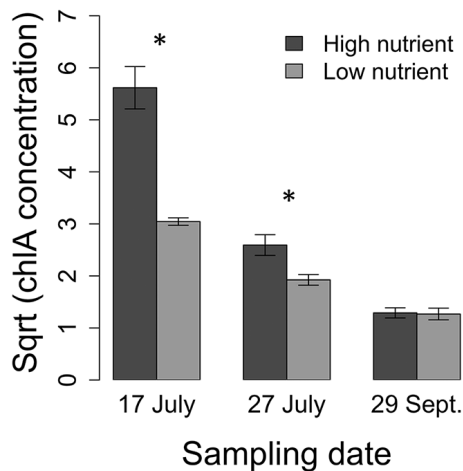

Fig. 2. Changes in the concentration of phytoplankton (measured by chlA) for the duration of our experiment in high- and low-nutrient treatments, averaged across invasive-species treatments. Sampling dates 17 July, 27 July, and 29 September correspond to days 10, 20, and 84 of the experiment. Asterisks above error bars indicate significant differences between high- and low-nutrient treatments within a sampling date. The asterisks indicate significant differences from the control in each treatment. Error bars indicate ± 1 standard error around the mean.

higher in the first sample compared to the second sample. There were no interactive effects of invasive species, nutrients, or time on zooplankton species richness. Zooplankton diversity increased over time but was not affected by invasive species, nutrients, or any treatment interactions.

Across all treatments, mean survival (±1 SE) of the three invasive species was 63% ± 9% for zebra mussels, 63% ± 7% for banded mystery snails, and 97% ± 2% for Asian clams (Table 3; Appendix S1: Fig. S5). None of the treatments affected zebra mussel or banded mystery snail survival. There was a significant effect of other invasive species on Asian clam survival (Table 3); however, none of the post hoc pairwise comparisons were different (all $P > 0.120$).

Zebra mussel and snail mass increased with added nutrients, but there was no effect of other invasive species or an interaction. Asian clam mass was not affected by nutrients, the other invasive species, or their interaction (Table 3; Appendix S1: Fig. S5).

Zebra mussel reproduction, which we quantified at the end of the experiment, was affected by the presence of the other invasive species ($F_{3,32} = 3.23$, $P = 0.035$), nutrients additions ($F_{1,32} = 3.32$, $P = 0.077$), and there was a significant species-by-nutrients interaction ($F_{3,32} = 3.26$, $P = 0.034$). Post hoc comparisons showed that zebra mussels only reproduced more in the high-nutrient treatment when combined with banded mystery snails ($P = 0.020$); all other treatments had similar amounts of reproduction ($P > 0.200$). In the high-nutrient treatment with banded mystery snails, two tiles had a low number of settled juveniles (zero and one), and three tiles had a higher number of settled juveniles (10, 54, and 74). Zebra mussels produced a mean (±1 SE) of 28 ± 17 settled juveniles (post-veliger stage) in the high-nutrient treatment in the presence of

Table 3. Results from each ANOVA on species survival and individual biomass.

Treatment	Mussel		Snail		Clam	
	F	P	F	P	F	P
Survival						
Nutrients (N)	$0.001_{1,31}$	0.996	$2.233_{1,32}$	0.145	$1.522_{1,32}$	0.226
Species (S)	$0.679_{3,31}$	0.572	$0.606_{3,32}$	0.616	$3.134_{3,32}$	**0.039**
N × S	$0.628_{3,31}$	0.603	$0.490_{3,32}$	0.692	$0.103_{3,32}$	0.958
Mass						
Nutrients (N)	$5.529_{1,31}$	**0.023**	$8.780_{1,32}$	**0.006**	$0.490_{1,32}$	0.491
Species (S)	$2.489_{3,31}$	0.078	$1.588_{3,32}$	0.212	$2.141_{3,32}$	0.114
N × S	$1.860_{3,31}$	0.157	$0.820_{3,32}$	0.493	$1.810_{3,32}$	0.165

Notes: The invasive species did not negatively affect one another in this experiment. Nutrient additions had a moderately positive effect on the growth of zebra mussels and banded mystery snails, indicating that these species might respond more favorably to nutrient pollution in freshwater systems. Values in subscript are df values. P values in boldface indicate statistical significance ($P < 0.05$).

banded mystery snails; all other treatments averaged less than one juvenile per tile.

DISCUSSION

We expected that zebra mussels and Asian clams would have the most significant effects on nutrient availability in the water column because of their effects on the distribution of nutrients in natural systems, transferring nutrients from the water column to the benthic community, leading to increased growth of periphyton (Cohen et al. 1984, Heath et al. 1995, Bastviken et al. 1998, Werner and Rothhaupt 2008, Vaughn and Hoellein 2018). This effect did not occur in our study. Of the three invasive species, banded mystery snails had the greatest effect on the abiotic aspects of the community by reducing TN and TP in high-nutrient conditions. Banded mystery snails might have egested a large portion of their (unprocessed) food intake, which would lock up nutrient resources until microbial decomposition occurred, limiting available nutrients for phytoplankton and reducing food resources for bivalves and zooplankton.

Regardless of nutrient inputs, filtering by Asian clams and zebra mussels should have reduced phytoplankton (the food resource for zooplankton), leading to a reduction in the density and species richness of zooplankton, which has been found in other mesocosm experiments (Dzialowski and Jessie 2009, Dzialowski 2013, Sinclair and Arnott 2015). Field observations indicate that the effects of invasive mollusks on

plankton communities can be highly variable, and not necessarily negative, even across a range of densities (Strayer et al. 2019). Of course, an increase or decrease in chlorophyll *a* does not necessarily correspond to an increase or decrease in biomass, count, or stoichiometry of the phytoplankton (Kruskopf and Flynn 2006, Huot et al. 2007). Additionally, chlorophyll concentrations can differ among mesocosms and natural conditions when nutrient concentrations are high (Dzialowski et al. 2014). Given the observed response of an increase in chlorophyll *a* with nutrients, and no change in chlorophyll *a* among the invasive-species treatments, we concluded that the filter feeders did not reduce the biomass of phytoplankton in our mesocosms. We also expected that additional nutrient inputs in the absence of invasive species would increase zooplankton abundance and species richness and that this positive effect of added nutrients would have been negated by the addition of Asian clams and zebra mussels, as shown in other mesocosm experiments (Dzialowski 2013, Sinclair and Arnott 2015). Yet, zebra mussels and Asian clams did not reduce phytoplankton, and we did not find any reductions of zooplankton. Our results differ from other studies that have suggested that Asian clams and zebra mussels reduce phytoplankton in experimental and natural freshwater systems (Dzialowski and Jessie 2009, Pigneur et al. 2014). Long-term research suggests that these effects might be highly variable, and not always negative (Strayer et al. 2019).

Our experimental manipulation was relatively short (87 d), but longer than other studies that observed effects of invasive bivalves on phytoplankton and zooplankton (e.g., Dzialowski and Jessie 2009, 25 d; Sinclair and Arnott 2015, 85 d). Zebra mussels and Asian clams might not reduce phytoplankton to the point where food resources are limiting for native filter feeders over long periods of time, which is supported by some evidence suggesting that the negative effects of zebra mussels on native species might be temporary (Strayer and Malcom 2007, Strayer et al. 2019). If the impacts of the invasive filter feeders used in our experiment were temporary and did not reduce resources to levels or for a length of time where competition led to the exclusion of native species, this would explain the lack of effects observed on the native zooplankton community. Invasive bivalves can dramatically alter natural freshwater ecosystems and community structure immediately after invading a system (e.g., benthic structure and water clarity; Strayer et al. 1999). The results of our experiment and other observational and experimental studies suggest that the effects of invasive mollusks on freshwater systems might be variable and context-dependent. The venue of research can affect the results and interpretation of results (Dzialowski et al. 2014); therefore, we remain cautious in our interpretation and extrapolation of these results to natural systems, mainly focusing on results founded on ecological principles.

Our results highlight the importance of using experiments to test the effects of invasive species reported by observational studies. Observational studies alone can imply that invasive species strongly affect native species and environmental conditions. We found that combined invasive mollusks did not have a stronger negative effect on abiotic and biotic aspects of the environment compared to a single invasive mollusk. Moreover, these results were consistent under high- and low-nutrient conditions. We expected that higher densities of invasive species would have stronger ecological effects on the mesocosms, regardless of species identity. More individuals in a mesocosm (e.g., 75 vs. 25) should consume more algae, and regardless of species identity would have negatively affected algal biomass or zooplankton biomass. We did not observe differences in algal biomass when 25, 50, or 75

individuals were present in the mesocosms, even when both bivalve species were present. Unfortunately, the additive experimental design used in this study does not allow us to test the mechanisms of species interactions. Nonetheless, it is unclear whether modifying the density of invasive species in this experiment would have identified mechanisms related to species interactions (i.e., competition or facilitation), given that density within a mesocosm has no biological relevance for density in lakes (Snaydon 1991).

As humans continue to alter aquatic ecosystems and transport non-indigenous species around the globe, novel interactions between invasive species will likely occur. Of the hypotheses proposed by Jeschke et al. (2012) to explain different ways that invasive species successfully invade a system, the invasional meltdown hypothesis (IMH) has the strongest empirical support (Simberloff and Von Holle 1999). The IMH predicts that invasive species within a habitat benefit one another through facilitative interactions; increasing the growth, reproduction, and distribution within the habitat. Additionally, invasive species increase the probability that additional non-native species successfully colonize the same habitat (Simberloff and Von Holle 1999). Despite some experimental and observational support for the IMH in some terrestrial systems (Aplet et al. 1991, O'Dowd et al. 2003, Relva et al. 2010), researchers continue to debate whether the IMH is supported by experimental and observational evidence in freshwater systems (DeVanna et al. 2011, Gallardo and Aldridge 2015, Jackson 2015, Meza-Lopez and Siemann 2015, Henriksson et al. 2016). Although some invasive species do facilitate one another (Gallardo and Aldridge 2015), human-induced changes to the environment might have a significant effect on the propensity and success of invasive species and determine the potential for facilitative interactions between invasive species. Future research efforts should focus on understanding if anthropogenic modifications to the environment are responsible for facilitative interactions among invasive species within the IMH framework.

Without considering how humans have altered environmental conditions, researchers might not be able to distinguish between the impacts of invasive species, and the trend that invasive

species tend to prefer highly degraded habitats (Didham et al. 2005, MacDougall and Turkington 2005). Zebra mussels generally need to attach to hardened substrates, and Asian clams tend to do better in areas that have plant-free, soft substrates. Dredged habitats, docks, and piers are primary examples of habitats that are highly modified in aquatic ecosystems where these invasive species would do well. Human modification of shoreline environments and the supplementation of limiting nutrients to freshwater ecosystems could be increasing the invasibility of freshwater systems and enhancing the effects of invasive species.

Given the context-dependent results in this experiment, we agree with Jackson (2015) that future research efforts should focus on understanding how complex native food webs are affected by the interactions between invasive species. Additionally, researchers should focus on how other human activities have modified freshwater ecosystems in ways that might inhibit or facilitate the success of invasive species and their effects of ecosystem functions and services. Also, our study did not focus on how varying densities of invasive species affect the environmental conditions. Altering densities of invasive species in experimental systems with variable anthropogenic effects (i.e., climate change, toxins, nutrients, road salt) could offer information about the potential effects that invasive species will have as humans continue to modify freshwater ecosystems around the world.

Acknowledgments

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Data Accessibility

Schuler, Matthew, et al. 2020. Data for the effects of nutrient enrichment and invasive mollusks on freshwater environments, Dryad, Dataset, https://doi.org/10.5061/dryad.gf1vhhmm0

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3196/full